1969

Larval development of Bathynectes superba (Costa) reared in the laboratory.

Morris H. Roberts Jr.
Virginia Institute of Marine Science

Reference: *Biol. Bull.*, **137**: 338–351. (October, 1969)

LARVAL DEVELOPMENT OF *BATHYNECTES SUPERBA* (COSTA) REARED IN THE LABORATORY [1]

MORRIS H. ROBERTS, JR.[2]

Virginia Institute of Marine Science, Gloucester Point, Virginia 23062

Larvae of several portunid species have now been described to varying extents by laboratory culture studies, including *Portunus puber* (egg to juvenile), *P. depurator* (egg to Zoea III), *Carcinus maenas* (egg to Zoea IV) by Lebour (1928), and *Callinectes sapidus* (egg to Zoea IV, Hopkins, 1943, 1944; egg to juvenile, Costlow and Bookhout, 1959). The first zoea of several additional species have been obtained from the egg, including *Bathynectes longipes,* several *Portunus* species, and *Polybius henslowi* (Lebour, 1928, 1931, 1944, 1950). Later stages of several species were described from larvae collected from the plankton, held through one or more molts and arranged in series up to a recognizable juvenile or adult form (Lebour, 1928,1944; Aikawa, 1929, 1933, 1937). Based on this work it is possible to identify many larvae in this family at least to genus. Early work does not provide information necessary to separate *Bathynectes* from other portunids because only the first stage was known and that incompletely described by present day criteria; thus Lebour (1928, 1931) was unable to distinguish *Bathynectes, Polybius,* and *Portunus.*

The present study was undertaken to determine the number of larval stages in *Bathynectes,* and to describe each larval stage in detail based on laboratory reared specimens. Criteria for distinguishing *Bathynectes* from other Portunidae were sought.

MATERIALS AND METHODS

An ovigerous *Bathynectes superba* was collected off the Virginia coast during a routine cruise in February, 1968, and brought to the laboratory in a small amount of water. The temperature at the collection station was about 10 C; the crab was maintained at this temperature during transit. The salinity was approximately 34‰. Water used for transporting the crab contained a considerable amount of mucous and fish scales, but the crab was alive and soon became active after being placed in a battery jar with clean ocean water at about 10 C.

The eggs were nearly ready to hatch, with eye spots, a beating heart, and larval pigmentation visible within each egg capsule. Some eggs were removed from the female and cultured using the procedures developed by Costlow and Bookhout (1960). Temperature was maintained at 10 C during incubation of the eggs. The female with the remainder of the egg mass was maintained in about 5 liters of water with daily water changes.

[1] Contribution Number 316 from the Virginia Institute of Marine Science, Gloucester Point, Virginia 23062.

[2] Present address: Department of Biology, Providence College, Providence, Rhode Island 02918.

After two days, weak pre-zoeae hatched from the egg mass on the female. During the following two days, Zoea I were obtained both from the female and from the incubated eggs. A total of 221 zoeae were segregated in compartmented plastic boxes, 2 zoeae per compartment. In addition, a large number (500–1000) were placed in mass culture in about 1 liter of water. Cultures were maintained in a cold room at 13 C or less for most of the culture period. Maximum temperature for the period was slightly above 16 C for one day. Nauplii of *Artemia salina* were provided as food. During the early part of the culture period, water collected at the same time and location as the ovigerous crab was used, with transfers every second day. On the fifteenth day, it became necessary to use water from Wachapreague Inlet, Virginia, concentrated to 34‰ by freezing and decanting. There was no marked change in mortality rate at this time.

Approximately 30 zoeae from the mass culture were preserved in 70% ethanol with 10% glycerol for detailed anatomical study along with dead specimens from the individual culture. Specimens of each stage were measured, and certain obvious details of setation and ornamentation noted. Figures of whole specimens and dissected appendages were made, and from these, plus notes made on several dissected specimens, descriptions of each stage were written and subsequently checked against additional specimens. All dissections were performed under 85% lactic acid. Measurements taken were: distance from tip of rostrum to tip of dorsal spine, length of rostrum, dorsal spine, and lateral spines, carapace length (tip of rostrum to posterior margin of carapace along mid dorsal line), abdominal length, and total length (carapace length plus abdominal length). The latter measurement is not exactly the "true" total length, but is the best possible approximation since the zoeae, living and dead, are so curved that no direct measurement is possible.

The following abbreviations are used throughout the paper: A 1 = antennule, A 2 = antenna, Mn = mandible, Mx 1 = maxillule, Mx 2 = maxilla, Mxp 1 = first maxilliped, Mxp 2 = second maxilliped, Mxp 3 = third maxilliped, P 1 to 5 = pereiopods 1 to 5, Pl 2 to 5 = pleopods 2 to 5, U = uropod.

Results

Five zoeal stages were obtained, the last one being terminal as judged by degree of development of pereiopod and pleopod buds. Unfortunately the megalopa was not obtained. Mean intermolt duration for each stage which molted was calculated from individual culture data: Zoea I, 8 days, Zoea II, 6 days, Zoea III, 7 days, Zoea IV, 11 days. One larva died 17 days after reaching Zoea V, without molting to the megalopa; most Zoea V's died after only 5 or 6 days.

Zoea I (Fig. 1)

Carapace (Fig. 1a) with rostral, dorsal, and lateral spines. Rostrum straight, strongly depressed. Dorsal spine long, strongly curved. Lateral spines short, strongly depressed, with very broad base giving carapace a flared appearance; lateral carapace margin with definite lobe below and behind eye. Eyes swollen, immobile. Abdomen (Fig. 1b) with 5 somites and telson. Two minute hairs

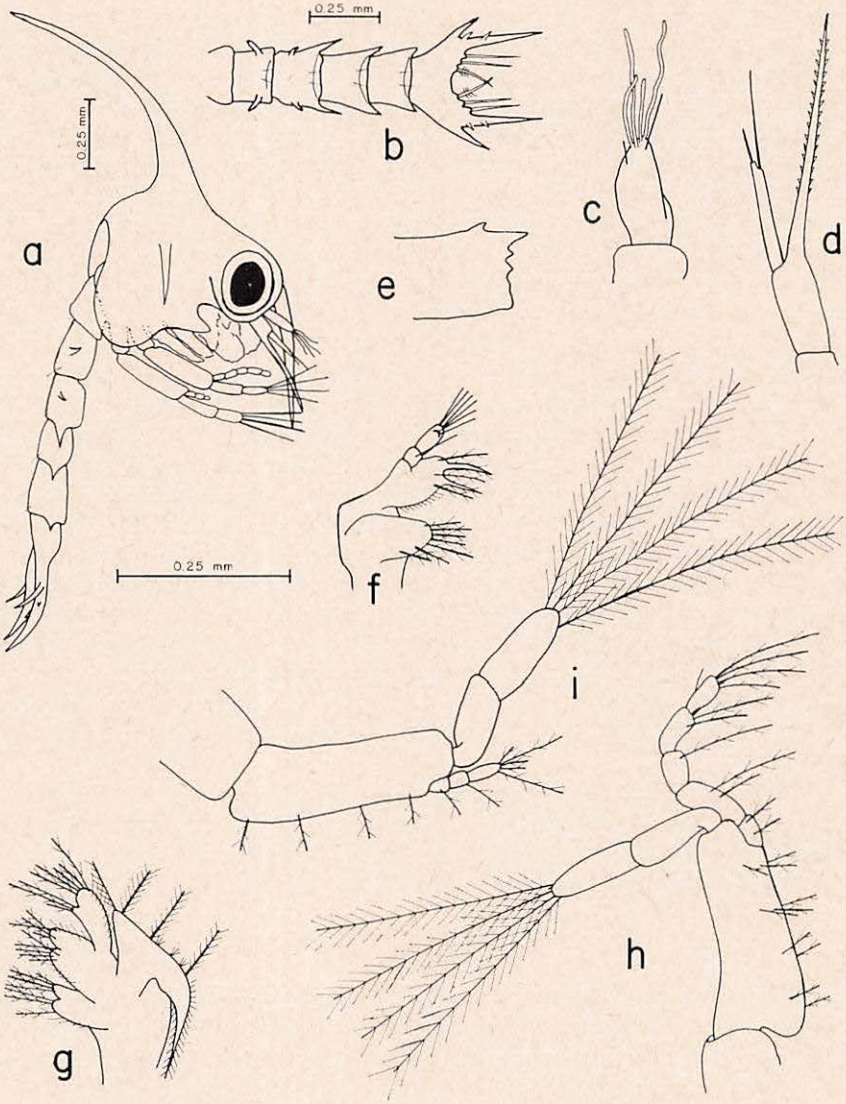

FIGURE 1. Zoea I of *Bathynectes superba*, a. lateral view, b. dorsal view of abdomen, c. antennule, d. antenna, e. mandible, f. maxillule, g. maxilla, h. first maxilliped, i. second maxilliped.

dorsally on second through fifth abdominal somites. Somites 3, 4, and 5 with long posterolateral spines, shortest on somite 5. Somites 2 and 3 with lateral knobs. Telson bifurcate, each furca with a long lateral spine curving dorsally plus 2 minute spines, 1 dorsal and 1 lateral. Furcal tips curved dorsally. Three median setae, articulated, with irregular setulation. No anal spine.

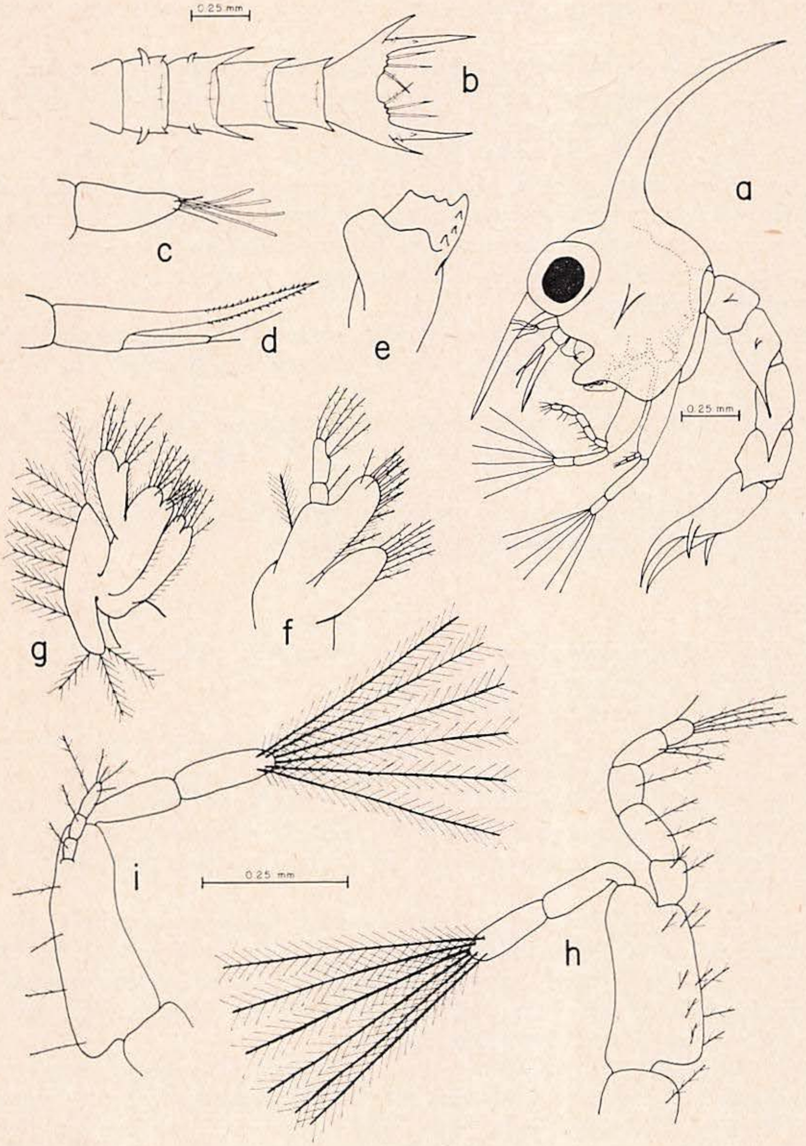

FIGURE 2. Zoea II of *Bathynectes superba*, a. lateral view, b. dorsal view of abdomen, c. antennule, d. antenna, e. mandible, f. maxillule, g. maxilla, h. first maxilliped, i. second maxilliped.

A 1 (Fig. 1c) Uniramous, with 4 terminal aesthetascs plus 2 setae.

A 2 (Fig. 1d)—Ventral peduncular spine with cuneate setules in 2 rows. Spine twice as long as exopod; exopod with 2 terminal setae, 1 long, 1 short. No endopod.

Mn (Fig. 1e)—Incisor process only, with 4 terminal teeth plus 1 tooth on posterior margin.

Mx 1 (Fig. 1f)—Coxal endite with 7 setae; basal endite with 5 setae; fringed with fine hairs on proximal margin. Endopod 2-segmented, with 4 terminal and 2 subterminal setae; 1 seta on proximal segment.

Mx 2 (Fig. 1g)—Coxal endite bilobed with 3 setae on proximal lobe, 4 on distal lobe; basal endite bilobed with 5 setae on proximal lobe, 4 on distal lobe; both endites fringed with fine hairs. Endopod unsegmented with 5 terminal setae and 3 setae on subterminal knob; margins fringed with fine hairs. Scaphognathite with proximal and distal lobes, 4 plumose setae; proximal lobe drawn out into long plumose projection.

Mxp 1 (Fig. 1h)—Coxa nude, basis with 10 setae on inner margin. Endopod with 2, 2, 1, 2, 5 setae on segments 1 to 5. Exopod 2-segmented with 4 terminal plumose setae.

Mxp 2 (Fig. 1i)—Coxa nude, basis with 4 setae on inner margin. Endopod with 1, 1, 5 setae on segments 1 to 3. Exopod 2-segmented with 4 terminal plumose setae.

Mxp 3—Very minute biarmous rudiment, smaller than Mxp 2 coxa.

P 1 to 5—Minute ridges the only visible rudiments.

Zoea II (Fig. 2)

Carapace, abdomen, and telson unchanged (Fig. 2ab). Eyes stalked.

A 1 (Fig. 2c)—Unchanged from Zoea I.

A 2 (Fig. 2d)—Unchanged from Zoea I.

Mn (Fig. 2e)—Incisor process with 4 terminal teeth and 3 teeth on posterior margin. Molar process now present.

Mx 1 (Fig. 3f)—Coxal endite with 7 setae; basal endite with 9 setae, fringed with fine hairs. Endopod with 4 terminal and 2 subterminal setae; 1 seta on proximal segment. A long plumose seta now present on basis proximal to endopod (epipodital hair).

Mx 2 (Fig. 2g)—Coxal endite bilobed with 3 setae on proximal lobe, 4 on distal; basal endite bilobed with 5 setae on each lobe; both endites fringed with fine hairs. Endopod with 5 terminal setae plus 3 setae on subterminal knob; both margins fringed with fine hairs. Scaphognathite with 10 plumose setate; proximal lobe not produced into a long projection.

Mxp 1 (Fig. 2h)—Coxa with 1 seta, basis with 10 setae on inner margin. Endopod with 2, 2, 1, 2, 5 setae on segments 1 to 5. Exopod with 6 terminal setae.

Mxp 2 (Fig. 2i)—Coxa nude, basis with 4 setae on inner margin. Endopod with 1, 1, 5 setae on segments 1 to 3. Exopod with 6 terminal plumose setae.

Mxp 3—Slightly larger biramous rudiment.

P 1 to 5—Buds enlarged, still smaller than Mxp 3 rudiment.

Zoea III (Fig. 3)

Carapace (Fig. 3a) unchanged except for thickening of dorsal spine. Abdomen (Fig. 3b) with 6 somites plus telson. Ornamentation unchanged from Zoea I except for slightly increased length of lateral spines on somite 4 and addition of

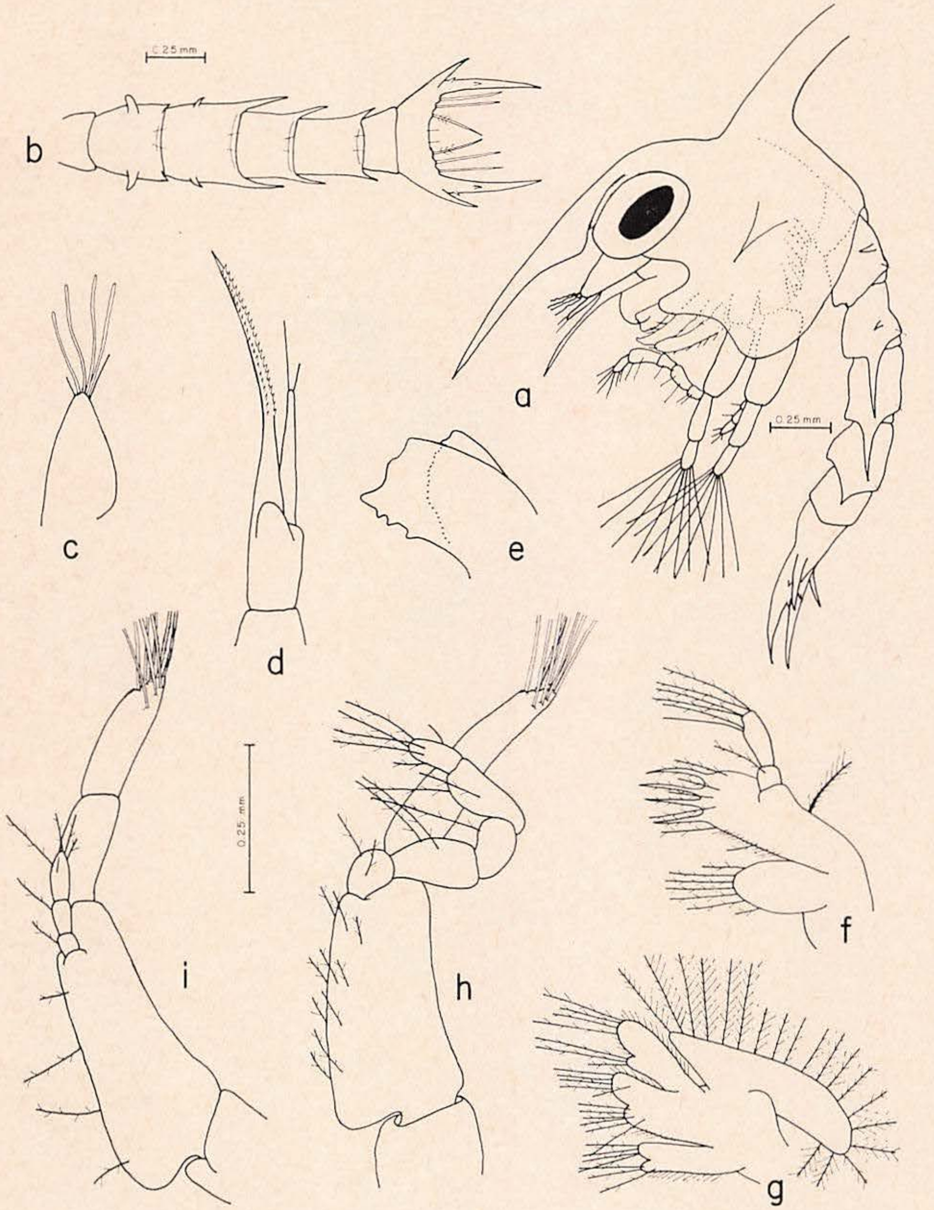

FIGURE 3. Zoea III of *Bathynectes superba,* a. lateral view, b. dorsal view of abdomen, c. antennule, d. antenna, e. mandible, f. maxillule, g. maxilla, h. first maxilliped, i. second maxilliped.

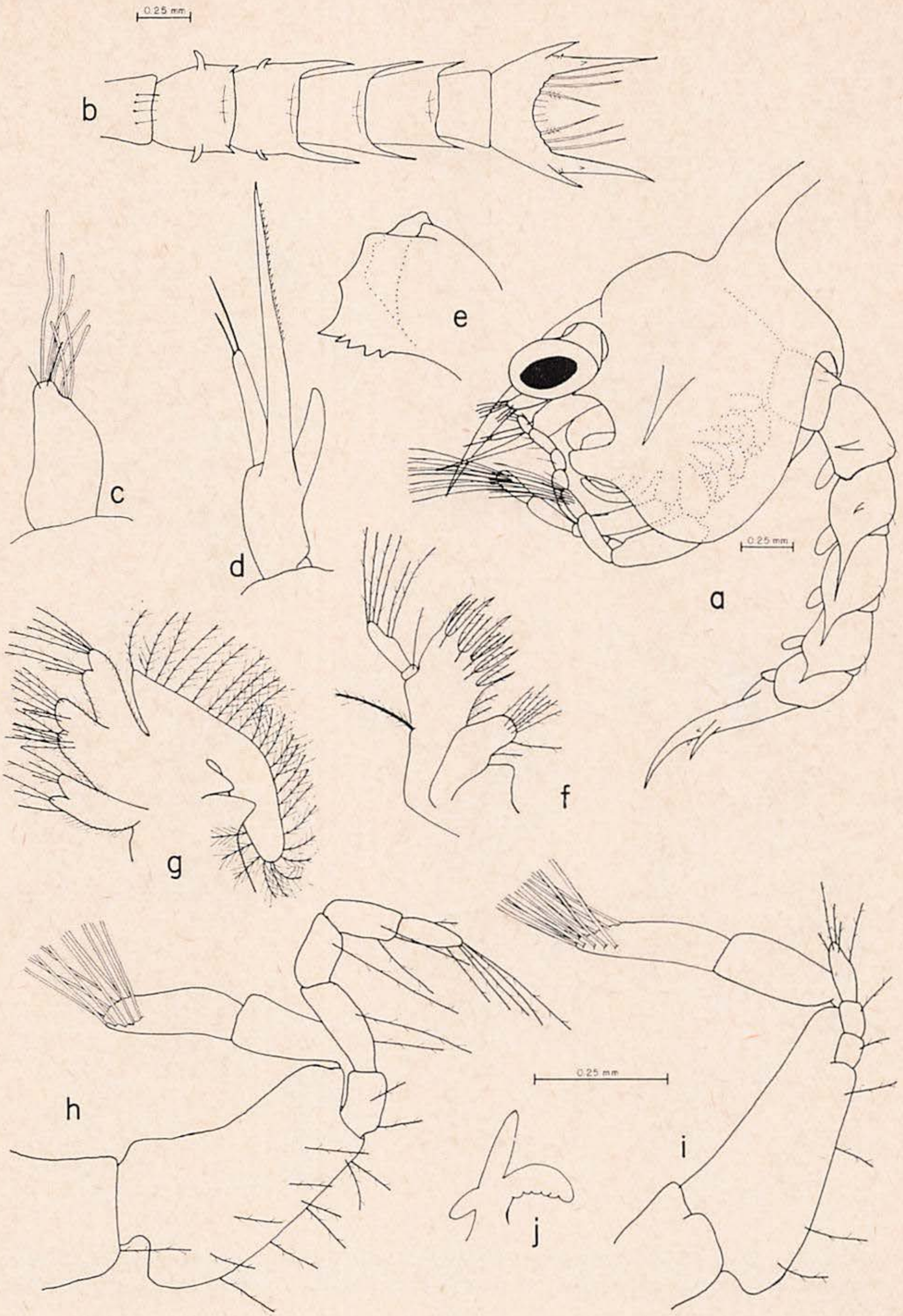

FIGURE 4. Zoea IV of *Bathynectes superba*, a. lateral view, b. dorsal view of abdomen, c. antennule, d. antenna, e. mandible, f. maxillule, g. maxilla, h. first maxilliped, i. second maxilliped, j. third maxilliped.

4 dorsal hairs on somite 1. Pleopod anlagen sometimes visible beneath exoskeleton. Telson still broad, with a pair of very short setae between the original three pairs.

A 1 (Fig. 3c)—Unchanged from Zoea I.

A 2 (Fig. 3d)—Unchanged from Zoea I except for addition of small endopod bud.

Mn (Fig. 3e)—Incisor process with 3 terminal teeth plus 3 teeth along posterior margin. Molar process with several teeth.

Mx 1 (Fig. 3f)—Coxal endite with 7 setae; basal endite with 10 setae, fringed with fine hairs. Endopod with 4 terminal and 2 subterminal setae; 1 seta on proximal segment. Epipodital hair present.

Mx 2 (Fig. 3g)—Coxal endite bilobed with 3 setae on proximal lobe, 4 on distal; basal endite bilobed with 6 setae on proximal lobe, 5 on distal; both endites fringed with fine hairs. Endopod with 5 terminal setae plus 3 setae on subterminal knob; margins fringed with fine hairs. Scaphognathite with 19 plumose setae, 6 long setae on distal lobe, 13 short setae on proximal lobe.

Mxp 1 (Fig. 3h)—Coxa with 1 seta, basis with 10 setae on inner margin. Endopod with 2, 2, 1, 2, 6 setae on segments 1 to 5. Exopod with 8 terminal plumose setae.

Mxp 2 (Fig. 3i)—Coxa nude, basis with 4 setae on inner margin. Endopod with 1, 1, 5 setae on segments 1 to 3. Exopod with 8 terminal plumose setae.

Mxp 3—Still a small biramous rudiment.

P 1 to 5—Rudiments slightly larger than Mxp 3.

Zoea IV (Fig. 4)

Carapace (Fig. 4a) with shield area prominently thickened; lateral marginal lobes prominent; 6 fine setae on posterolateral area near margin, on inner surface, directed medially (not readily visible, unfigured). Abdominal somites unchanged (Fig. 4b). Telson with a second pair of short setae medially.

A 1 (Fig. 4c)—Uniramous, with 4 aesthetascs and 2 setae terminally, 3 aesthetascs subterminally.

A 2 (Fig. 4d)—Unchanged from Zoea III except endopod bud considerably larger, about $\frac{1}{2}$ exopod.

Mn (Fig. 4e)—Unchanged from Zoea III.

Mx 1 (Fig. 4f)—Coxal endite with 9 setae; basal endite with 16 setae, fringed with fine hairs. Endopod with 4 terminal and 2 subtermial setae; 1 seta on proximal segment. Epipodital hair present.

Mx 2 (Fig. 4g)—Coxal endite bilobed with 3 setae on proximal lobe, 4 on distal; basal endite bilobed with 7 setae on each lobe; both endites fringed with fine hairs. Endopod with 5 terminal setae and 3 setae on subterminal knob; margins fringed with fine hairs. Scaphognathite with 27 plumose setae, 10 long setae on distal lobe, 17 short setae on proximal lobe.

Mxp 1 (Fig. 4h)—Coxa with 1 seta, basis with 10 setae on inner margin. Endopod with 2, 2, 1, 2, 6 setae on segments 1 to 5. Exopod with 10 terminal plumose setae.

Mxp 2 (Fig. 4i)—Coxa nude, basis with 4 setae on inner margin. Endopod with 1, 1, 5 setae on segments 1 to 3. Exopod with 10 terminal plumose setae.

FIGURE 5. Zoea V of *Bathynectes superba*, a. lateral view, b. dorsal view of abdomen, c. antennule, d. antenna, e. mandible, f. maxillule, g. maxilla.

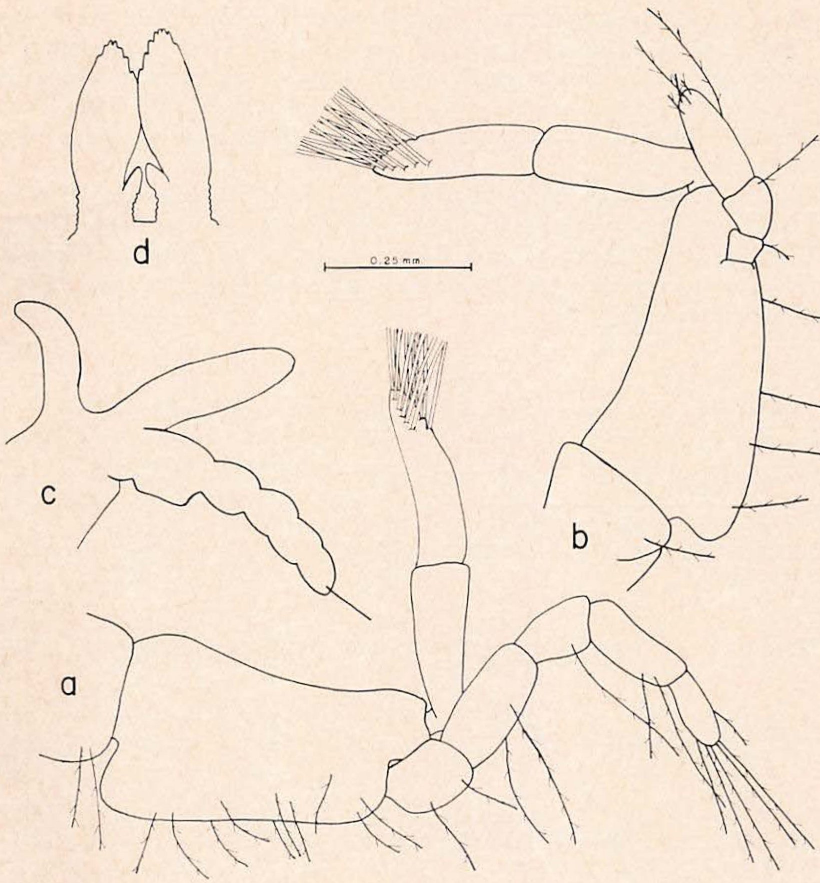

FIGURE 6. Zoea V of *Bathynectes superba*, a. first maxilliped, b. second maxilliped, c. third maxilliped, d. pleopod buds, abdominal somite 4.

Mxp 3 (Fig. 4j)—Rudiment triramous; endopod wrinkled, curved medially; exopod straight; epipod curved posteriorly into branchial chamber. No setae on rami.

P 1 to 5—Greatly enlarged; pseudosegmented; P 1 with biramous tip or chela. P 5 hidden behind P 2 to 4.

Pl 2 to 5 (Fig. 4a)—Small uniramous buds; medially located on somites.

U—Small uniramous bud; laterally positioned on somite 6.

Zoea V (Figs. 5 and 6)

Carapace and abdomen (Fig. 5a, b) unchanged from Zoea IV; 8 setae on posterolateral region of carapace.

A 1 (Fig. 5c)—Biramous, 4 aesthetascs and 2 setae terminally, 8 aesthetascs subterminally, 5 distally, 3 proximally. Inner ramous present as small subterminal palp.

A 2 (Fig. 5d)—Unchanged from Zoea IV except endopod bud about $\frac{3}{4}$ spine.

Mn (Fig. 5e)—Incisor process with no terminal teeth but 8 teeth along posterior margin. Molar process with several teeth. Palp present, unsegmented.

Mx 1 (Fig. 5f)—Coxal endite with 13 setae; basal endite with 19 setae. Endopod with 4 terminal and 2 subterminal setae; 1 setae on proximal segment. Epidopdital hair present.

Mx 2 (Fig. 5g)—Coxal endite bilobed with 5 setae on each lobe; basal endite bilobed with 8 setae on proximal lobe, 9 on distal; both endites fringed with fine hairs. Endopod with 5 terminal and 3 subterminal setae; margins fringed with fine hairs. Scaphognathite with 42 plumose setae, 14 long setae on distal lobe, 28 short setae on proximal lobe.

TABLE I

Zoeal dimensions with mean, observed range, and number measured for each stage

Zoea	Rostrum to dorsal spine	Rostrum	Dorsal spine	Lateral spine	Carapace length	Abdominal length	Total length
I	1.75	0.40	0.85	0.26	0.64	1.37	2.01
	1.62–1.80	0.36–0.46	0.72–0.90	0.23–0.29	0.61–0.72	1.30–1.44	1.98–2.12
	24	25	24	19	25	25	25
II	1.94*	0.55	0.81*	0.27	0.85	1.55	2.41
	1.82–2.06	0.52–0.61	0.69–0.96	0.22–0.28	0.81–0.96	1.38–1.71	2.20–2.64
	15	28	15	30	30	30	30
III	2.38*	0.62	0.97*	0.26	1.17	1.75	2.93
	2.25–2.61	0.45–0.72	0.81–1.17	0.22–0.31	1.08–1.26	1.62–1.89	2.70–3.06
	19	30	19	27	28	30	28
IV	3.26	0.84	1.56	0.33	2.00	2.36	4.41
	3.03–3.44	0.83–0.88	1.24–1.68	0.28–0.36	1.73–2.20	2.20–2.61	4.04–4.68
	21	21	21	21	21	21	21
V	3.75	1.00	1.65	0.34	2.44	2.68	5.13
	3.58–3.99	0.86–1.03	1.51–1.79	0.28–0.41	2.26–2.53	2.48–2.75	4.95–5.28
	24	27	26	27	27	26	26

* Probably underestimated since the specimens measured were primarily from mass culture in which most had damaged dorsal spines resulting from attempted cannibalism.

Mxp 1 (Fig. 6a)—Coxa with 2 setae, basis with 10 setae on inner margin. Endopod with 2, 2, 1, 2, 6 setae on segments 1 to 5. Exopod with 12 terminal plumose setae.

Mxp 2 (Fig. 6b)—Coxa with 1 seta, basis with 4 setae on inner margin. Endopod with 1, 1, 5 setae, on segments 1 to 3. Exopod with 12 terminal plumose setae.

Mxp 3 (Fig. 6c)—Endopod with 5 pseudosegments, proximal (ischium) slightly broadened; 1 terminal seta. Exopod straight, nude. Epipod curved posteriorly into branchial chamber, nearly equals exopod, nude.

P 1 to 5—P 1 chelate, segmented; P 2 to 5 all segmented, pointed. Nearly fill central carapace space.

Pl 2 to 5 (Fig. 6d)—Biramous, lacking setae but with small knobs terminally.
U—Unchanged from Zoea IV.

It is clear from the degree of development observable in Mxp 3, P 1 to 5, Pl 2 to 5, and U, that this is the last zoeal stage, even though no megalopa was obtained. Thus like *Portunus, Bathynectes* has five zoeal stages.

Pigmentation: Black chromatophores were present in all zoeal stages on the basis of Mxp 1 and 2, the inner mouth parts, the labrum, ventrally on the cephalothorax, around the intestine, and posteroventrally on abdominal somites 3, 4, and 5. Eyes were dark brown. Abdominal somite 1 had a red-brown chromatophore. The telson was diffused with a pinkish hue. In Zoea IV, small yellow or white chromatophores were noted on the branchial and posterior regions of the carapace (very inconspicuous). They may have been present earlier, but were not noted. In Zoea V the chela of P 1 had a red-orange chromatophore as did the 6th abdominal somite, and in some cases the other pereiopods. At no time did the carapace bear any characteristic black chromatophores. Unlike Lebour's *B. longipes* Zoea I, larval *B. superba* did not have a chromatophore in the middle of the dorsal spine.

Mean dimensions of each zoeal stage along with the observed ranges and number of specimens measured are summarized in Table I. The zoeae increased from about 2 mm total length in Zoea I to about 4.4 mm in Zoea V. Growth increments were not linear but markedly saltatory with a very pronounced increase from Zoea III to Zoea IV of about 1.5 mm, all other growth increments being less than 1 mm. The same marked jump in growth increments was observed in every dimension measured. Examination of Lebour's (1928) body length data for *Portunus puber* shows the same phenomenon at the same place in the developmental sequence. No measurements were givn for *Callinectes sapidus* (Costlow and Bookhout, 1959), but a gross comparison of the figures of each stage suggests a similar jump in growth increment between Zoea IV and Zoea V, this latter species having 7 instead of 5 stages. This appears to be characteristic of this family, not having been reported in any other group.

Discussion

Lebour (1928) published a brief description and line drawing of the first zoea of *Bathynectes longipes* and later (1931) a colored figure. From this information there seems to be a distinction in pigment pattern between the larvae of *B. longipes* and *B. superba*. There is a distinct black chromatophore on the dorsal spine of *B. longipes* which is not present in *B. superba*. In addition, *B. longipes* seems to have more pigment overall than *B. superba*.

In external anatomy, the two species are more similar. A completely detailed comparison is not possible since *B. longipes* was not described in great detail nor are more than the first zoea known. Body length (total length less rostrum) of *B. longipes* Zoea I is about 0.5 mm less than *B. superba* Zoea I. In both species, the rostrum-dorsal spine length equals the body length. Carapace spines are in both cases strongly curved. The lateral spines are relatively long in both species, with a lateral spine:rostrum ratio of about 1:2 in *B. longipes, ca.* 3:5 in *B. superba*. This ratio is gradually reduced in *B. superba* to only 3:10 in Zoea IV. In Zoea I of both species, the A 2 exopod:peduncular spine ratio is *ca.* 1:2, endopod absent, peduncular spine nearly reaching rostral tip. The telson cannot be compared as it does not show clearly in the figures of *B. longipes*. There appear to be no posterolateral spines on abdominal somites 3, 4 and 5 in *B. longipes* while at least the first two of these spines are well developed in *B. superba* in Zoea I and all three in later instars.

Lebour (1928) indicated such great similarity between *Bathynectes* and *Portunus* as to preclude separation. Both have five zoeal stages; carapace with rostral, dorsal, and lateral spines; A 2 with truncated exopod, long peduncular spine, and endopod absent in early stages, developing in later stages; abdomen and telson similar. Aikawa (1937) claimed a difference in type of A 2 between *Bathynectes* and *Portunus* but this was most certainly unjustified both from Lebour's (1928, 1931, 1944, 1950) figures and consideration of *B. superba*.

There are differences between these two genera which, if they hold up as more species of *Portunus* become known, should permit separation. *Bathynectes* has a relatively longer lateral carapace spine than has *Portunus;* lateral spine:rostrum ratio equal to or greater than 1:2 in *Bathynectes* Zoea I, much less than 1:2 in *Portunus*. Even in later stages, there is probably a difference despite the reduction in this ratio in *Bathynectes*. The A 2 exopod:peduncular spine ratio is equal to 1:2 for *Bathynectes,* between 1:4 and 1:2 for *Portunus*. The posterolateral abdominal spines seem slightly better developed in *Bathynectes,* but this may result from inaccuracies in available *Portunus* descriptions. *Bathynectes* has 1 dorsal and 2 lateral spines on the telson furcae, one of the lateral spines (in *B. superba* at least) being very long. *Portunus* has only 2 lateral spines on the furcae of many species, 3 in some cases, but only in *P. spinimanus* (Lebour, 1950) is there a spine anywhere near as long as that of *Bathynectes*. As more larvae are described in better detail, additional differences will probably be detected.

Based on the description and figures of Costlow and Bookhout (1959), the same characteristics that distinguish *Bathynectes* and *Portunus* will also separate *Bathynectes* and *Callinectes*. *Callinectes* has seven zoeal stages compared to five for *Bathynectes* and *Portunus*. Therefore zoeae of *Callinectes* at comparable stages of development of pereiopod and pleopod buds will have more natatory setae on the Mxp exopods than the other two species. *Callinectes* has extremely short lateral spines, with a lateral spine:rostrum ratio of only 1:5 compared to 1:2 in *Bathynectes*. *Callinectes* has long posterolateral spines on abdominal somites 3, 4, and 5 in all stages, all three being about the same length, while they are all small in Zoea I of *Bathynectes* and the last one is smaller than the other two in all stages. The A 2 exopod of *Callinectes* is truncated with 2 unequal setae as in *Bathynectes* and *Portunus,* but the exopod:peduncular spine ratio is less than 1:4.

Bathynectes and *Carcinus maenas,* belonging to different subfamilies within the Portunidae, are more readily separated. *Carcinus* has only 4 zoeal stages before the megalopa. It lacks lateral carapace spines and postero-lateral spines on abdominal somites 3, 4, and 5. These differences have already been pointed out by Lebour (1928).

I would like to express my appreciation to the Ichthyology Department and particularly Mr. John McEachran who kindly brought me the ovigerous female.

I also appreciate the advice of Dr. Fenner A. Chace on several taxonomic questions. During the study I was the recipient of a National Science Foundation Graduate Fellowship.

SUMMARY

1. The external anatomy of 5 zoeal stages of *Bathynectes superba* is described from laboratory-reared specimens. Based on Mxp 3, P 1 to 5, Pl 2 to 5, and U structure in Zoea V, it is concluded that this is the last zoeal stage even though no megalopae were obtained.

2. It is suggested that *Bathynectes* can be distinguished from *Portunus* and *Callinectes* by differences in lateral carapace spine:rostrum ratio, A 2 exopod:peduncular spine ratio, spination of telson, and relative lengths of lateral abdominal spines.

LITERATURE CITED

AIKAWA, H., 1929. On larval forms of some Brachyura. *Rec. Oceanogr. Works Jap.*, **2**: 17–55.

AIKAWA, H., 1933. On larval forms of some Brachyura II. A note on indeterminate zoeae. *Rec. Oceanogr. Works Jap.*, **5**: 124–254.

AIKAWA, H., 1937. Further notes on Brachyruan larvae. *Rec. Oceanogr. Works Jap.*, **9**: 87–162.

COSTLOW, J. D., JR., AND C. G. BOOKHOUT, 1959. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. *Biol. Bull.*, **116**: 373–396.

COSTLOW, J. D., JR., AND C. G. BOOKHOUT, 1960. A method for developing brachyuran eggs *in vitro*. *Limnol. Oceanogr.*, **5**: 212–215.

HOPKINS, S. H., 1943. The external morphology of the first and second zoeal stages of the blue crab, *Callinectes sapidus* Rathbun. *Trans. Amer. Microscop. Soc.*, **62**: 85–90.

HOPKINS, S. H., 1944. The external morphology of the third and fourth zoeal stages of the blue crab, *Callinectes sapidus* Rathbun. *Biol. Bull.*, **87**: 145–152.

LEBOUR, M. V., 1928. The larval stages of the Plymouth Brachyura. *Proc. Zool. Soc. London,* **1928**: 473–560.

LEBOUR, M. V., 1931. Further notes on larval Brachyura. *Proc. Zool. Soc. London,* **1931**: 93–96.

LEBOUR, M. V., 1944. Larval crabs from Bermuda. *Zoologica,* **29**: 113–128.

LEBOUR, M. V., 1950. Notes on some larval decapods (Crustacea) from Bermuda. *Proc. Zool. Soc. London,* **120**: 369–379.